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# Soft-bodied fossils from the roof shales of the Wigan Four Foot coal seam, Westhoughton, Lancashire, UK

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**Abstract** – Exceptionally preserved fossils are described from the Westhoughton opencast coal pit near Wigan, Lancashire, UK (uppermost Westphalian A, Lower *Modiolaris* Chronozone, *regularis* faunal belt). The fossils occur within sideritic concretions in a 1.5-metre zone above the Wigan Four Foot coal seam. Arthropods dominate the fauna and include arachnids, arthropleurids, crustaceans, eurypterids, euthycarcinoids, millipedes and xiphosurans. Vertebrates are represented by a single palaeoniscid fish, numerous disarticulated scales and coprolites. Upright *Sigillaria* trees, massive bedded units and a general lack of trace fossils in the roof shales of the Wigan Four Foot coal seam suggest that deposition of the beds containing these concretions was relatively rapid. Discovery of similar faunas at the equivalent stratigraphic level some distance away point to regional rather than localized controls on exceptional preservation.

## 1. Introduction

Recent investigations of new Upper Carboniferous fossil localities in the West Lancashire Coalfield have produced significant results (Anderson *et al.* 1997). We now report new discoveries from an opencast coal pit at Westhoughton, in the northwest of England (Fig. 1). The Westhoughton locality, situated approximately three miles east of Wigan (Grid Reference 669 004, Landranger 109), consisted of a large opencast mine operated by Rackwood Minerals Ltd. from June 1995 until backfilling in early 1997. A preliminary account of the geological setting of the locality appeared in Dunlop & Horrocks (1996), who described a new specimen of the trigonotarbid arachnid *Maiocercus*. Dunlop & Horrocks (1997) subsequently described a new species of phalangiotarbid arachnid from this site.

The opencast mining operations at Westhoughton provided a unique opportunity to study Coal Measure fossils collected *in situ* (they are more commonly found in spoil heaps; Jarzembowski, 1989) and to 'dissect' geologically a Fossil Konservat-Lagerstätte, a site where exceptional preservation prevails, and soft-bodied organisms normally absent from the fossil record are preserved. This project aimed to determine the detailed stratigraphy, geological setting and preservational environment of the site, and to report the exceptionally well-preserved fossils.

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Prior to Anderson *et al.* (1997), it was generally believed that exceptionally preserved fossils in Lancashire were restricted to the Sparth Bottoms brick clay pit, Rochdale and the Soapstone bed of the Burnley district (both Westphalian A). As the arachnid *Maiocercus* had previously been recorded from Westhoughton, an investigation of the new excavation was essential, and initial collections of concretions confirmed the presence of such fossils. Material described here and prefixed LL reside with the Carl Horrocks Collection (Manchester Museum, University of Manchester).

## 2. Geological setting

Opencast mining at Westhoughton permitted a detailed stratigraphy of the site to be constructed. Three coal seams were worked, the deepest being the Trencherbone seam, followed by the Wigan Two Foot and finally the Wigan Four Foot (Fig. 2). Initially, it was thought that the roof shales of all these coals might yield fossiliferous concretions. However, the contribution from the roof shales of the Wigan Four Foot far outweighed that from the rest.

Jones, Tonks & Wright (1938) broadly outlined the nature of the Wigan Four Foot roof shales in the West Lancashire coalfield, whilst the sedimentological character of the roof shales was mapped by Broadhurst and France (1985, their fig. 4a). Sandstone predominates to the northwest in the worked area of the Bickershaw and Parsonage collieries, whereas to the

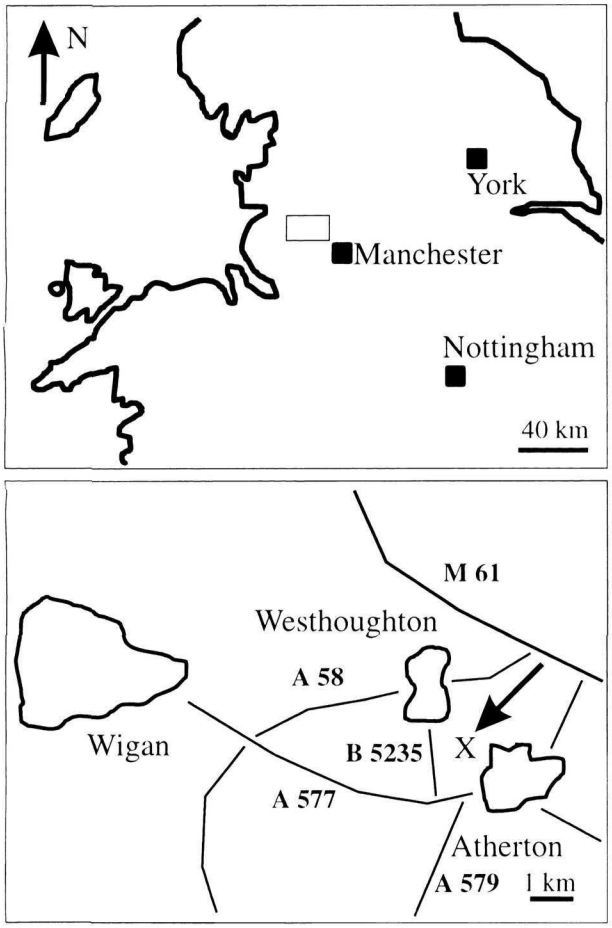


Figure 1. (a) Regional location map of the Westhoughton coal pit (study area indicated by box). (b) Specific location map showing the position of the site relative to the local road network.

south and southwest, from Parkside Colliery for some 10 km to the southeast, the roof is of shale. A thin band of non-marine shells lies in the roof shales in the Westhoughton–Atherton area, and can be found as far south as Old Boston, south of Ashton (Jones, Tonks & Wright 1938). The non-marine fauna is best known from records at Hewlett No. 2 Pit, Hart Common, two kilometres west-southwest of Westhoughton, where two individual horizons were found, at 46 cm and 61 cm above the top of the coal, separated by about 7 cm of barren shale. The lower leaf yielded a fauna of medium-to-large *Carbonicola* of the *C. communis* group including *C.* aff. *os-lancis* characteristic of the *crista-galli* Faunal Belt of the basal *Modiolaris* Chronozone. The upper leaf was characterized by the distinctive small species *Carbonicola venusta* of the succeeding *C. venusta* Faunal Belt of W. B. Wright of the lower *Modiolaris* Chronozone. Examination of non-marine bivalves from the roofs of the Wigan Four Foot at Westhoughton revealed the presence of *Anthracosia* cf. *regularis* (Figs 3a, b).

We examined the Wigan Four Foot interval in particular detail to determine possible associations between the fossils and the small-scale stratigraphy. Detailed sedimentary logging of the interval above the Wigan Four Foot identified two broad patterns. Firstly, individual nodule size increases up succession from diameters of 2–3 cm to greater than 50 cm. Secondly, fossil content changes noticeably up through the succession. With increasing height above the coal seam, plant fossils become less common, and many nodules contain no visible organic remains at all. The Wigan Four Foot roof shales mark a coarsening up cycle, culminating in cross-bedded sands hosting *Stigmaria ficoides* and *Calamites*. The *Calamites* trunks show a marked angle of inclination, which we interpret as indicating the prevailing transport direction of the sediment that engulfed them, suggesting a relatively rapid rate of deposition for this unit. Trace fossils are uncommon, but towards the top of the roof shales, small *Arenicolites carbonarius* occur.

The Wigan Two Foot seam was truncated towards the north of the site by a channel with associated fills including basal shale rip-up clasts. The Wigan Two Foot nodules tended to be composed of coarser grained material than those of the Wigan Four Foot. This grain-size difference allowed nodules found on the spoil tips to be assigned confidently to each respective seam. Rippled sandy silts lying above the Wigan Two Foot seam are infrequently traversed by the xiphosuran walking trace *Kouphichnium* ichnosp. The fauna preserved in concretions are sparse and typically include pygocephalomorph shrimps and xiphosurans.

The Trencherbone seam formed the floor of the opencast, and attained a total thickness of about 1.05 m. Sideritic nodules from the roof shales of the Trencherbone were typically 2–3 cm in diameter, and yielded plant material (mainly *Cyperites*), a few xiphosurans (*Liomesaspis* and *Bellinurus*) and pygocephalomorph shrimps. The Trencherbone roof-shale nodules were identified amongst tip material by their characteristic dark blue-gray outer surfaces. The strata immediately above the Trencherbone seam lie at the base of the *Carbonicola crista-galli* faunal belt (Upper Westphalian A). Magraw and Calver (1960) noted that the *Vanderbeckei* Marine Band (Westphalian A–Westphalian B boundary) occurs within the interseam sequences separating the Wigan Four Foot and Lower Florida seams. Thus, we confidently assign the exceptional biota to an uppermost Westphalian A age.

With ongoing excavation at Westhoughton, the quality and availability of exposures changed from week to week. However, careful recording of available exposure at any one time, produced a detailed picture of the stratigraphy, which is summarized in Figure 2.

## 3. Preservation

Fossils from Westhoughton occurred within variably sized flattened siderite concretions. The exceptions were pygocephalomorph shrimps preserved in shales, and a single *Cyclus* crustacean from within an upright

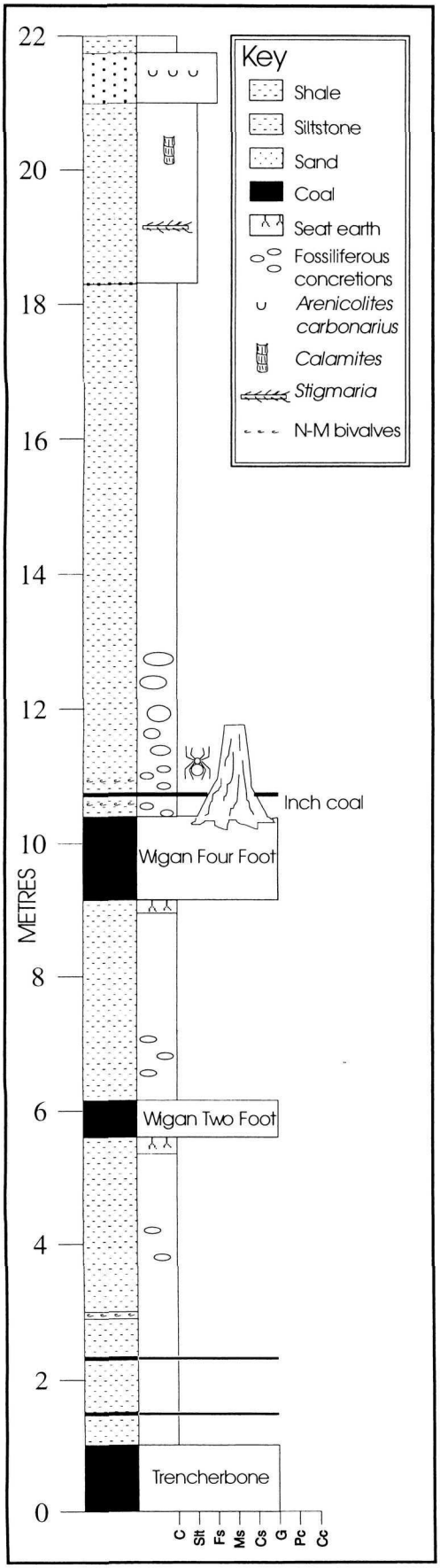


Figure 2. Stratigraphic log of the sequence exposed at Westhoughton, showing the position of the fossil-bearing sideritic concretions, the Wigan Four Foot, the Wigan Two Foot and the Trencherbone coal seams. Abbreviations: C is clay, Slt is siltstone, Fs is fine sand, Ms is medium sand, Cs is coarse sand, G is granules, Pc is pebble conglomerate and Cg is cobble conglomerate.

tree trunk in the Wigan Four Foot roof shales. Isolated fossil shrimps were previously recorded from coal-bearing sequences by Eagar & Li (1993), and this may be due to their preferential preservation compared to unmineralized forms.

Within the siderite concretions, there often occurs an infill of kaolinitic material that also hosts minor galena, chalcopyrite, pyrite and rare sphalerite, in addition to calcite and pink dolomite. These minerals are most often encountered within concretions containing three-dimensional *Lepidostrobus* cones, but also occur along jointing planes within the blocky sandstone overlying the Wigan Four Foot roof shales. Some of the larger sideritic concretions are septarian in nature, the vugs filled with a mixture of pink dolomite, calcite, chalcopyrite and solidified bitumen. The high proportion of well-preserved terrestrial animals collected from the site, most of which possess some degree of soft-tissue mineralisation, coupled with the presence of *in situ* tree trunks, tends to suggest that these faunal elements experienced little transport.

## 4. Palaeontology

### 4.a. Plants

Although this study concentrated on the discovery of soft-bodied animals, fossil-plant remains within the concretions were also considered in order to avoid collection bias with identifications based on Cleal & Thomas (1994). Plant-bearing concretions were scarce at Westhoughton in comparison to Bickershaw (Anderson et al. 1997). Ferns were very rare, with only occasional *Mariopterus* fronds recovered. One of the most common plant fossils were *Lepidostrobus* cones from a level approximately 105 cm above the Wigan Four Foot coal seam. Other finds from within concretions included *Trigonocarpus* and *Cyperites*. *Calamites* and *Stigmaria ficoides* with permineralized cell structure were found *in situ* within the upper portion of the Wigan Four Foot roof shales, where they became more sandy in composition. Finally, upright *Sigillaria* trees were found rooted within the Wigan Four Foot coal seam.

### 4.b. Non-marine bivalves

Non-marine bivalves are represented at Westhoughton by *Carbonicola* of the *C. venusta* group of W. B. Wright, the shells of which were subsequently assigned to early *Anthracosia* of the group *A. regularis* (Figs 3a, b) (see also Eagar, 1977). They include several small *Anthracosia* of the *A. modiolaris* group, three *Naiadites* aff. *flexuosus* (Figs 3d, e), and a number of

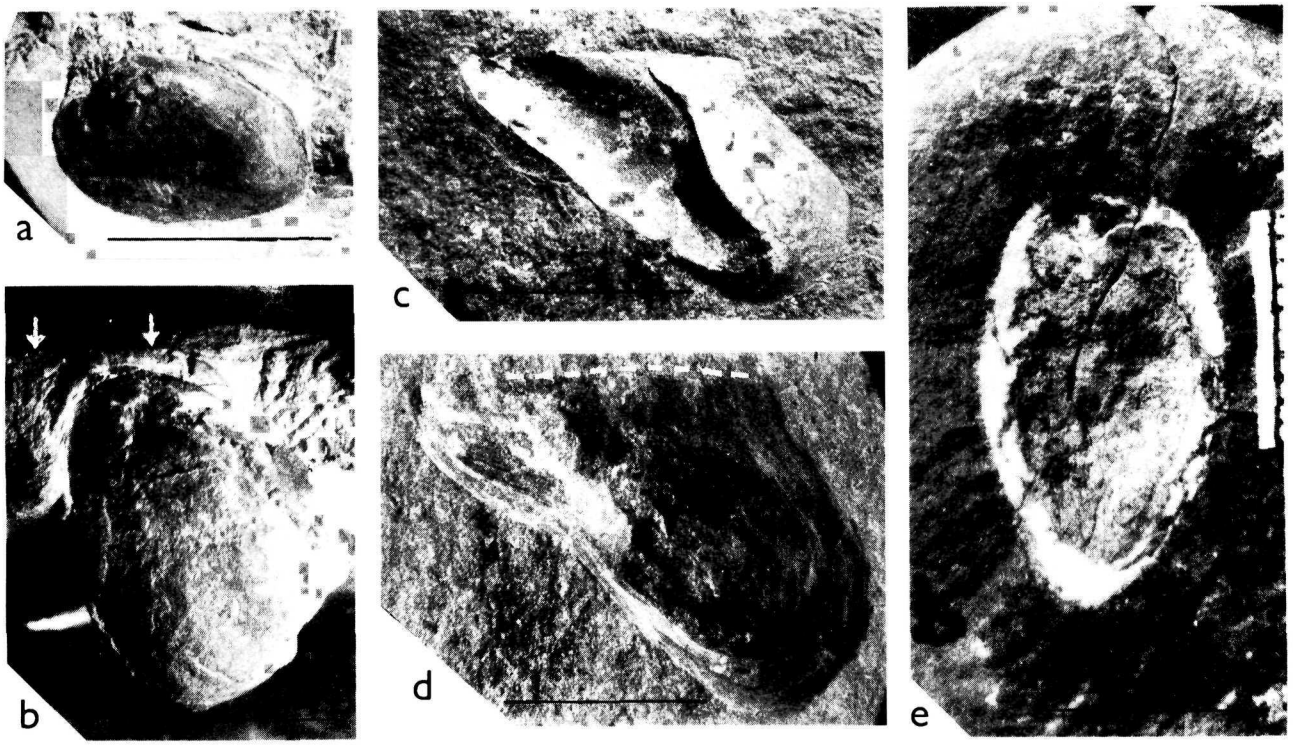


Figure 3. Non-marine bivalves from the roof shales of the Wigan Four Foot coal seam. (a) *Anthracosia* cf. *regularis* (Trueman). 3b. *A.* aff. *regularis*, a shell in a steeply dipping position. The line of bedding is indicated by arrows. (c and d). *Naiadites* aff. *flexuosus* Dix and Trueman, oblique varieties. The broken line in (d) outlines the hinge margin. (e) Cross section of a large shell in a steeply dipping position; the plane of the bedding is at right angles to the page. The curved fractures in the shell suggest shears due to compaction. Scale bars are 1 cm.

large broken shells of *Curvirimula* sp. With the exception of the latter, Jones, Tonks & Wright (1938) reported this fauna only from the upper leaf of the band at Hart Common, located some two kilometres west of Westhoughton, the lower leaf showing a fauna belonging to the underlying *crista-galli* faunal belt.

*Curvirimula* is a new record on the horizon of the Wigan Four Foot coal seam, and occurs mingled with all the remaining faunal elements of the upper leaf. Its presence in the roof shales of the coal suggests the former existence of a fluvio-deltaic regime during deposition. A similar palaeoenvironmental interpretation was deduced for the well-preserved fossils from above the Haigh Yard Coal by Anderson *et al.* (1997). Study of the bivalves by one of us (RMCE) indicates that some of the *in situ* shells are in steeply dipping orientations with respect to bedding (Fig. 3b). This orientation strongly suggests that the bivalves were in the process of escaping upwards to keep pace with the heavy sedimentation. The fact that the anthracosiids are relatively small, but have high shell-height to shell-length, and shell-length to length of anterior shell-end values (see Eagar, 1994), is also typical of stunting under heavy sedimentation.

#### 4.c. Arachnids

Arachnids recorded from Westhoughton include trigonotarbids, an extinct group of spider-like arachnid. *Maiocercus celticus*, a species originally recorded from the Westhoughton area as *M. orbicularis* by Gill (1911), was described and figured from a new, almost complete specimen (LL11143) from the site by Dunlop & Horrocks (1996). Dunlop & Horrocks (1996) also noted two less well-preserved specimens (LL 11144, 11145). A total of seven specimens of this species have now been recovered from Westhoughton. In addition to *Maiocercus*, an isolated opisthosoma is referred to *Cryptomartus* sp.

Phalangiotarbids (Fig. 4a), an extinct arachnid group of uncertain affinity, were described by Dunlop & Horrocks (1997) as *Mesotarbus peteri* sp. nov. Four specimens were figured by the authors (LL 11149–11152), and additional specimens exist in the Manchester Museum collection (LL 11147, 11148, 11306). There is also a probable ricinuleid (LL 11146), an order of arachnids with extant representatives (Selden 1992).

Scorpion fossils from Westhoughton include a small carapace (LL 11339) approximately 8 mm wide, with a teardrop-shaped eye tubercle close to its anterior margin, provisionally referred to *Eoscorpius* sp. (see Kjellesvig-Waering (1986). Baldwin & Sutcliffe (1904) recorded *Eoscorpius* from Sparth Bottoms, Rochdale. There are also fragments of much larger scorpions, including a post-abdominal segment about 1 cm wide (LL 11330) that belonged to an animal about 15 cm long (Pocock, 1911; Kjellesvig-Waering, 1986), an

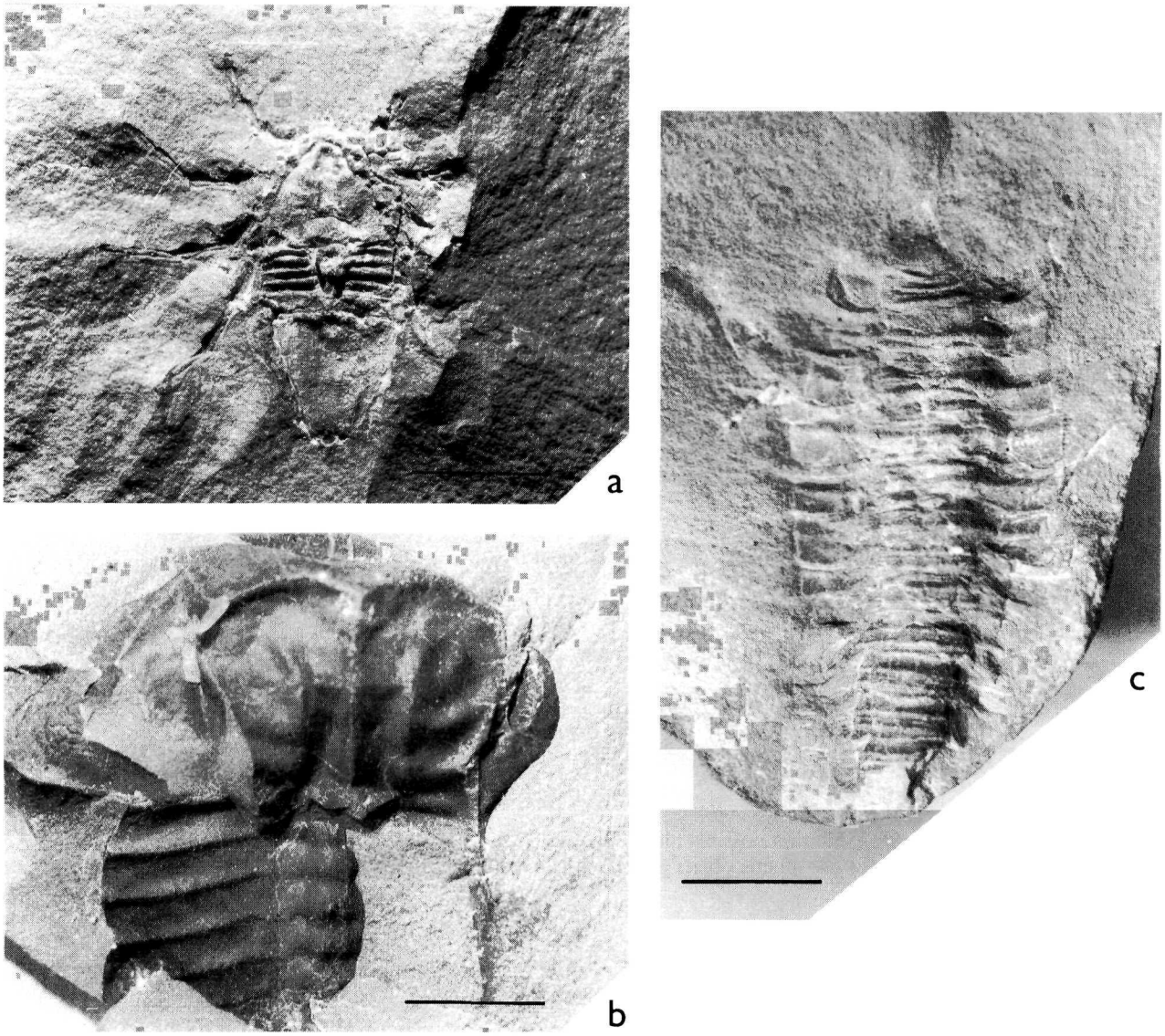


Figure 4. (a) Dorsal view of the phalangiotarbid arachnid *Mesotarbus peteri* Dunlop and Horrocks (1997). (b) Dorsal view of the xiphosuran *Euproops rotundatus* Prestwich (1840), showing a prominent ophthalmic spine on the right-hand side of the carapace. (c) The rare syncarid crustacean *Pleurocaris annulatus* from equivalent-aged strata at Cranberry Lea Farm, Lancashire. Scale bars are 1 cm.

isolated tergite nearly 2 cm wide (LL 11329), and three associated tergites (each about 1.5 cm long) in a block of plant-rich roof shale (LL 11326). These larger fragments scale up to an animal 15–20 cm long. Scorpions of this size have previously been recorded from the Upper Carboniferous (A. Jeram, pers. comm., 1995), but have not been named.

#### 4.d. Eurypterids

A large fragment of a distal arthropod leg (LL 11340), consisting of a large subtriangular segment with a curving claw and a smaller, socketed spine, is identified as eurypterid in origin. Of the two lineages surviving into the Upper Carboniferous period, the *Anthraconectes* morphotype and the larger *Hibbertopterus* morphotype (S. J. Braddy, unpub. Ph.D. thesis, Univ. Manchester, 1996), our new leg fragment is most similar to the end of leg 5 of *Anthraconectes* (Wills, 1964, text-fig 6). *Anthraconectes* eurypterids are typically about 10 cm long excluding the telson, but this fragment scales up to an animal nearer 30 cm long, and is possibly the largest example of an *Anthraconectes* type eurypterid yet recorded.

#### 4.e. Xiphosurans

Three xiphosurans (horseshoe 'crabs') have been recovered from Westhoughton: *Bellinurus trilobitoides*, *Euproops rotundatus* and *Liomesaspis laevis*. These are the typical species encountered from rocks of this age throughout UK and European coalfields. Specimens

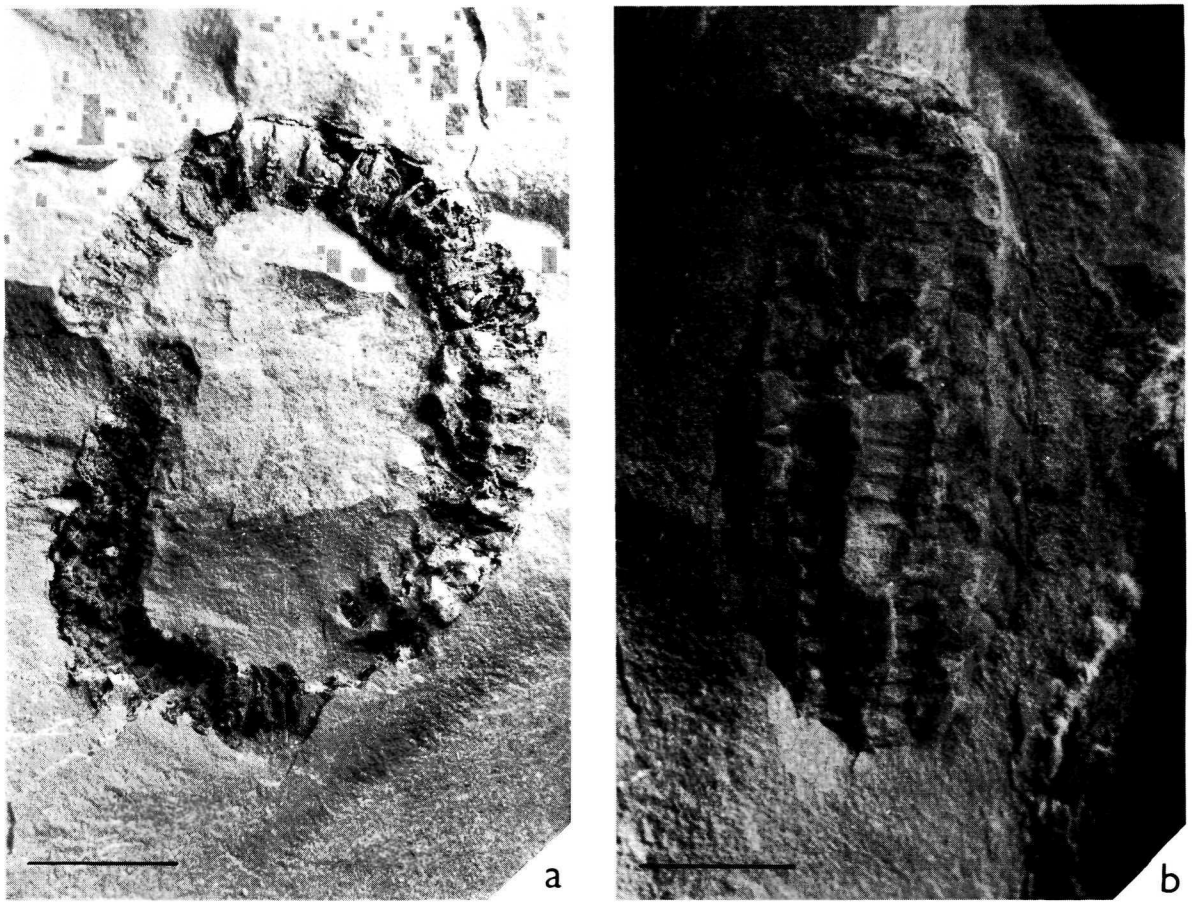


Figure 5. (a) *Xyliolius* millipede exhibiting possible phosphate preservation of soft part tissues. (b) The enigmatic arthropod *Camptophyllia* with a cigar-shaped phosphatic object preserved towards the posterior of the animal, interpreted as a mineralized gut fill. Scale bars are 1 cm.

of *Bellinurus trilobitoides* (LL 11275–11282) tend to be very poorly preserved, often no more than a pyritized film even within siderite concretions. In addition to single occurrences, two concretions containing multiple exoskeletons were found (LL 11154, 11155). Interestingly, the individuals within these concretions all appear to be loosely enrolled. In contrast, specimens of *Euproops rotundatus* (LL 11283–11289) tend to be well preserved (see Fig. 4c), perhaps as a result of an originally thicker exoskeletal cuticle, and include two loosely enrolled individuals (LL 11288, 11289). The third xiphosuran, *Liomesaspis laevis*, is represented by only a few specimens from this site and was the subject of a recent taxonomic revision by Anderson (1997).

#### 4.f. Myriapods

Millipedes are represented at Westhoughton by seven reasonably complete specimens, all of which are referred to *Xyloiulus* sp. This genus is diagnosed on segments with prozonites and metazonites of a similar diameter and a distinctive pattern of striations running along the length of the body parallel to its axis (Hoffman, 1969). The millipedes tend to be preserved as partial-cuticle, partial-kaolinitic/calcitic infills. MM LL 11294 (Fig. 5a) exemplifies the mode and quality of preservation of millipedes from this site.

Arthropleurids (giant multipodous Palaeozoic arthropods) were recently described from the Somerset coalfield by Proctor (1998), who, after examining plant-arthropod assemblages at Writhlington and reviewing previous work, suggested that they may have occupied levee forest habitats. Arthropleurids are represented from Westhoughton by a single large isolated paratergal plate and many small body fragments. The presence of numerous upright *Sigillaria* trees above the Wigan Four Foot coal seam indicates a former forest habitat, and that the arthropleurid material has not been transported very far from its source of origin.

#### 4.g. *Camptophyllia*

A single specimen of the unusual arthropod *Camptophyllia eltringhami* Gill (1924) was recovered from Westhoughton (LL 11153) (Fig. 5b). Although showing similarities to both isopod crustaceans (Gill, 1924) and arthropleurids (Brooks, 1962), the affinities and mode of life of *Camptophyllia* remain uncertain. This new specimen is particularly unusual as it appears

to show phosphatized gut contents, though no details of diet have yet been distinguished. *Camptophyllia* was previously described from the Lancashire coal field by Hansman (1972).

#### 4.h. Euthycarcinoids

Two euthycarcinoids (LL 11327, 11328) identified as *Smithxerxes pustulosus* Schram & Rolfe (1982) were discovered. LL 11328 is the first specimen from the UK to show well-preserved appendages. The affinities and mode of life of euthycarcinoids remain controversial, although they are generally considered to be aquatic arthropods. *Smithxerxes* also occurred at Bickershaw (Anderson *et al.* 1997).

#### 4.i. Crustaceans

The phyllocarid *Dithyrocaris* is represented at Westhoughton by one specimen (LL 11308), identified by the distinctive carapace, telsonic spines and preservation style. The enigmatic crustacean *Cyclus* is represented by a single specimen, which was preserved within an *in situ Sigillaria* tree trunk. Schram, Vonk & Hof (1997) argued that cycloid crustaceans bore remarkable convergent similarities to the body plan of crabs. It is interesting that the Westhoughton specimens were found within the cast of an upright *Sigillaria* tree. The sediment infilling the tree trunk moulds displayed faint lamination indicative of periodic sedimentation, and it may be that the hollow trunks acted as sumps into which organisms were washed and preserved.

#### 4.j. Vertebrates

A single, complete palaeonisciform fish (LL 11156), identified by its distinctive scale type, was discovered. Concretions were also found containing larger isolated scales, and loose groups of scales which probably belong to *Platysoma* (M. Coates, pers. comm. 1996) and possibly *Rhizodus*. Schultze & Maples (1992) pointed out that Carboniferous Lagerstätten sites rich in vertebrates are commonly poor in invertebrates due to the preferential preservation of phosphatic remains. The situation appears reversed here, where only a small fraction of the preserved fauna is vertebrate in origin.

#### 4.k. Coprolites

Coprolites at Westhoughton, are represented by phosphatic 'blobs' ranging in size from about 1–15 cm in diameter. These include specimens showing what appear to be fragments of terrestrial millipedes, arachnids and xiphosurans. Spiral coprolites, recorded from Bickershaw by Anderson *et al.* (1997) are only very rarely encountered within the Westhoughton concretions, indicating differing faunal composition at these different localities.

Table 1. Material collected from Cranberry Lea Farm exposures

| Taxa | Collection number |
|---|---|
| *Pleurocaris annulatus* (syncarid shrimp) | LL 11162, LL 11266 |
| *Dithyrocaris* sp. | LL 11274 |
| Pygocephalomorph shrimp | LL 11163 |
| Ostracodes | LL 11318–LL 11320 |
| *Palaeoxyris* (shark egg capsule) | LL 11264 |
| *Bellinurus trilobitoides* | LL 11267, 11279, 11315 |
| *Euproops rotundatus* | LL 11265 |
| Insect wing fragment | LL 11269 |
| *Liomesaspis laevis* | LL 11268, LL 11272, LL 11309–LL 11311, LL 11316 |

## 5. Geographical extent of the Westhoughton biota

At the time of investigation, one other exposure of the Wigan Four Foot seam was accessible. This was an opencast pit operated by Rackwood Minerals Ltd. at Cranberry Lea Farm, near Ashton-in-Makerfield, Wigan District, Lancashire, approximately 11 kilometres southwest of Westhoughton. The Wigan Four Foot roof shales again yielded both aquatic and terrestrial animals, but due to the temporary nature of the site, there was less opportunity to sample the fauna and so comparisons between the sites were limited. All of the Cranberry Lea Farm material was collected loose from the spoil tips and cannot be accurately positioned above the Wigan Four Foot coal seam. However, this additional locality points to the Wigan Four Foot Konservat-Lagerstätte as being a geographically widespread phenomenon. The most significant finds from Cranberry Lea Farm are listed in Table 1.

## 6. Regional setting

The equivalent fauna preserved at Cranberry Lea Farm indicates that localized flooding of low-lying areas, perhaps as a result of storms, is an unlikely explanation for this occurrence. A more general explanation is required for the apparent basin-wide rise in water level at the time of deposition of the Wigan Four Foot roof shales.

Hartley (1993) outlined a depositional model for equivalently aged strata (Westphalian A to Westphalian B) in the South Wales coal field, which may in part explain some of the observations made at Westhoughton. He postulated that there may have been a eustatic origin to parasequences containg coal seams during this stratigraphic interval. By interpreting non-marine bivalve horizons as up-dip equivalents of marine bands, it is possible to outline the following series of events.

Relative sea-level rise incurs groundwater-level rise inland from the coast, flooding previously vegetated areas represented here by the upright, rooted trees and coal. Water-table rise may have formed a brackish or freshwater lake with low levels of clastic input, ideal for colonisation by non-marine bivalves. At Westhoughton, important evidence of the water salin-

ity comes from the bivalve *Curvirimula*, which is thought to have had a higher salinity tolerance than most other Upper Carboniferous non-marine forms (see comment by Eagar in Broadhurt, Simpson & Hardy, 1980). Formation of a lake produced conditions that were amenable for the deposition and subsequent preservation of the terrestrial arthropods, as well as the resident crustaceans, xiphosurans and non-marine shells. Subsequent to colonisation by the non-marine shells, sedimentation rate must have increased, perhaps as a result of re-establishment of river deltas building out into the lake, which effectively killed off these localized faunas. Eventually, clastic input into the lake was such that an emergent surface was formed, which was once again colonized by terrestrial vegetation and animals represented by the upright *Calamites*.

Future research may be able to delineate the lateral extent of the Westhoughton biota and investigate whether original topographic features of the submerged landscape influenced the distribution of this style of deposit. However, this remains impracticable until further opencast mines are opened to exploit the Wigan Four Foot seam.

## 7. Comparisons

Upper Carboniferous Konservat-Lagerstätten have many characteristics in common, aside from preservation in siderite concretions. One of these is the presence of *in situ* trees defining a vertical fossiliferous zone with examples recognized from the Mazonian Delta Complex (Baird *et al.* 1985), Sparth Bottoms, and the Swillington brick clay pit near Leeds (Scott 1984). Broadhurst and Magraw (1959) noted that tree casts are not particularly rare within coal-bearing rocks, citing an example from the Blackrod No. 2 Opencast Mine northeast of Wigan, and pointing out the significance of this occurrence in terms of rapid sedimentation rates. To be preserved, the trees must have been buried prior to decomposition, and this in turn is reliant on a relatively fast deposition rate. As such, upright trees above coal seams may be useful palaeobotanical pathfinders to exceptional preservation.

Specific comparisons of faunal elements occurring at these sites are difficult due to the spread of stratigraphic ages involved. Schultze and Maples (1992) used cluster analysis to compare nine Pennsylvanian (Westphalian D) vertebrate localities, and produced a ranking scheme between marine- and freshwater-influenced depositional environments. All of the UK sites are vertebrate-poor, and experience gained from field collection at Westhoughton and Bickershaw suggests that this is not due to collection bias, but actual absence. Consequently, for Westhoughton to be compared to the scheme of Shultze and Maples (1992), it must be by virtue of the arthropod assemblages. When this is done, the biota is identified as lying closest to the terrestrial / freshwater end-member.

Table 2. Abundance of unmineralized arthropod taxa from Westhoughton

| Aquatic | | Terrestrial | |
|---|---|---|---|
| *Bellinurus* | c. 30 | *Maiocercus* | 7 |
| *Euproops* | 6 | *Cryptomartus* | 1 |
| *Liomesaspis* | 2 | *Mesotarbus* | 12 |
| *Smithxerxes* | 2 | Large scorpions | 2 |
| *?Anthraconectes* | 1 | ?Ricinuleid | 1 |
| *Cyclus* | 1 | *Xyloiulus* | 7 complete (c. 50 incomplete) |
| | | *Arthropleura** | 3 |
| | | *Camptophyllia** | 1 |

* The mode of life of both *Arthropleura* and *Camptophyllia*, i.e. aquatic, amphibious or terrestrial, remains uncertain.

Finally, comparing the Westhoughton and Bickershaw biotas highlights a major difference, namely that there are far more aquatic arthropods and fewer terrestrial arthropods at Bickershaw (see Table 2). This suggests that even within two sites of roughly equivalent age, which would normally be described collectively as a Braidwood-type fauna, there are subtle palaeoecological differences reflecting original site location relative to river channels and the interface with marine waters. We argue that the conventional two-fold division of this style of Konservat-Lagerstätten into Essex and Braidwood (terrestrial and freshwater) biotas is an oversimplification of an essentially gradational series between two end-members.

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